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THREE NEW SPECIES OF *DIPLACUS* (PHRYMACEAE) RELATED TO *D. CUSICKII* AND *D. NANUS*

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ABSTRACT

Three new species of *Diplacus* are described. *Diplacus cusickii* proves to be narrowly endemic to northern Malheur Co., Oregon, and a few localities in immediately adjacent Idaho along the Snake River; populations outside of this area previously identified as *Mimulus cusickii* are described here as **Diplacus cusickioides** Nesom, **sp. nov.** Plants of the Malheur County population system (*D. cusickii* sensu stricto) were identified by Thompson as intermediate between *Mimulus cusickii* and *M. nanus* and the lectotype that he selected for *Eunanus cusickii* Greene is from this same population system. **Diplacus deschutesensis** Nesom, **sp. nov.**, from Crook, Deschutes, Jefferson, Klamath, Lake, and Wheeler counties, Oregon, was regarded by Thompson (2005) as a zone of stabilized hybrids intermediate also between *Mimulus cusickii* [= *D. cusickioides*] and typical *M. nanus*. The *D. deschutesensis* population system lies mostly southwest of the range of *D. cusickioides* and intermediates apparently are few if any. Specimens are cited for the narrow Nevada endemic *Diplacus ovatus*, which Thompson treated as intermediate between *D. cusckii* [= *D. cusickioides*] and *D. nanus* var. *mephiticus*. **Diplacus cascadensis** Nesom, **sp. nov.**, from Deschutes, Klamath, and Lake counties, Oregon, has mostly been identified as *Mimulus nanus*. Ezell (1971) proposed to treat these plants at subspecific rank within *M. nanus* but the Oregon endemic is distinct from typical *D. nanus* in morphology and geography. Whether or not the evolutionary origin of *D. deschutesensis*, *D. cusickii*, and *D. ovatus* involved hybridization, each behaves as a distinct species.

KEY WORDS: *Mimulus*, *Diplacus*, Oregon, Oregon, Idaho

David Thompson's detailed and authoritative monograph (2005) of *Mimulus* subgenus *Schizoplacus* (recently considered by Barker et al. 2012 to be the separate genus *Diplacus* Nutt.) greatly advanced the understanding of the taxonomy of that group. Thompson's approach was conservative — he recognized 30 species, including only two previously undescribed taxa, both at varietal rank. Tulig and Nesom (2012) and Nesom (2013b) revived 8 species of sect. *Diplacus* that were treated by Thompson either at varietal rank within *Mimulus aurantiacus* or not recognized by him at all. In other groups of *Diplacus*, Nesom (2012) raised three taxa to specific rank, including both of Thompson's new varieties. *Diplacus thompsonii* Nesom (Nesom 2013a) as regarded by Thompson (2005) as a system of intermediates between *D. nanus* var. *mephiticus* and *D. bigelovii*. In the present study, three previously undescribed species are recognized as species — two of them were regarded informally by Thompson as population systems of intermediates or stabilized hybrids, while the third had been recognized by Ezell (1971) as a subspecies of *Mimulus nanus* but never formally published. The genus currently is regarded to include 48 species (Nesom 2013).

Diplacus cusickii is a narrow endemic primarily of Malheur County, Oregon

Thompson (2005) noted that collections in northern Malheur Co., Oregon, were intermediate between *Mimulus cusickii* and *M. nanus*. He cited and mapped such populations from Malheur Co. and adjacent Ada Co., Idaho, along the Snake River. These plants have abruptly and sharply acuminate leaf apices like *D. cusickii*, but they differ in having glabrous leaf surfaces and the corolla tube is yellow-bottomed with red spots, this feature especially prominent in dried corollas of herbarium specimens.

Because typical *Diplacus nanus* occurs in close sympatry with these populations (see citations below) and because of the tightly coherent geography of the population system, my initial interpretation was that the northern Malheur County plants were reasonably recognized as a species distinct from the more widespread "*D. cusickii*." Upon studying the lectotype of *D. cusickii* (*Eunanus cusickii* Greene) at UC, it was apparent that Greene's name applies to the narrowly endemic population system. The morely widely distributed species, which is thus without a name, is described below as *D. cusickioides*, maintaining the tribute to William Cusick and keeping the two entities closely associated in herbarium arrangements.

DIPLACUS CUSICKII (Greene) Nesom, Phytoneuron 2012-39: 28. 2012. *Eunanus cusickii* Greene, Pittonia 1: 36. 1887. *Mimulus cusickii* (Greene) Rattan, Analytical Key West Coast Bot. (ed. 3), 63. 1898. **LECTOTYPE** (Thompson 2005, p. 82): **USA. Oregon**. Malheur Co.: sandy hills of the Malheur, Jun 1885, *W.C. Cusick 1262* (UC!; isolectotypes: GH, ORE!, OSC!, PH!).

Greene's protologue: "Oregon and Washington Territory: collected by Cusick and by Howell. The species a most beautiful one, lacking the villous pubescence of *E. bigelovii* and otherwise different." Thompson's lectotypification (p. 87) was thoroughly considered and is repeated here: "Of the specimens I saw, only the following specimens have dates and collectors suitable for consideration as syntypes for this name: Interior of Oregon, 1885, *Howell s.n.* (K!); Oregon, John Day Valley, Muddy Station, 12 May 1885, *Howell s.n.* (BM! GH! MIN! NY-2! ORE! OSC! PH! WS! WTU!); Oregon, "Sage planes [sic]," 16 Jun 1885, *Howell s.n.* (GH!); Oregon, Deshutes [sic] bridge, 19 Jun 1885, *Howell s.n.* (BM! NY-3! ORE! PENN! PH! WS!); and the lectotype collection, *Cusick 1262*, cited above. Of these, only two are labeled "*Eunanus cusickii*" or "*E. cusickii*" in Greene's hand (*Cusick 1262*; OSC, UC). I cannot regard any particular one of the Howell specimens as a syntype, because Greene did not annotate them and his protologue citations are too vague; some of the specimens he studied may have been lost in the 1906 fire at CAS. Piper (1906) listed *Cusick 1262* as the type collection, but did not specify a particular specimen as the lectotype. I have selected the UC specimen of this collection to serve as the lectotype, since it is located where Greene worked at the time and is annotated by him."

Annual herbs, taprooted. **Stems** erect to erect-ascending, 1–8 cm, minutely stipitate-glandular with hairs 0.1–0.2 mm long. **Leaves** basal and cauline or mostly cauline, (10–)15–25(–35) mm x 4–17 mm, relatively even-sized or gradually larger distally, congested at crowded distal nodes, blades ovate to broadly elliptic-ovate, proximal with a short petiole-like base 1–5 mm, midstem and distal sessile, margins entire, short-stipitate-glandular, apex acuminate to a sharp point, both surfaces glabrous or adaxial minutely (microscopically) stipitate-glandular. **Flowers** (1–)2 per node, chasmogamous. **Fruiting pedicels** 1–1.5 mm. **Calyces** 7–10 mm, not inflated in fruit, glabrous to minutely (microscopically) stipitate-glandular, lobes triangular acuminate, unequal, usually falcate-spreading, apices linear-acuminate, sharp-pointed. **Corolla** magenta or rose-purple, tube yellow, throat color, throat and distal tube red-spotted on floor, palate ridges yellow, densely villous, tube-throat 13–16(–19) mm, floor hairy with fine hairs, limb 16–24 mm wide, distinctly 2-lipped. **Anthers** included, glabrous to sparsely hirsutulous. **Style** pubescent, at least on distal half; stigma slightly exserted, lobes subequal, slightly longer than upper anthers (herkogamous), lobe margins densely short-ciliate. Capsules 10–15 mm, usually exceeding the calyx.

Flowering May–Jul. Slopes, canyons, washes, irrigation ditches, sand talus, diatomaceous slopes, basalt outcrops, black volcanic gravel, volcanic ash and sand, usually in sagebrush areas; 800–1000 m. Idaho, Oregon.

Specimens examined. **Idaho**. Ada Co.: Snake River Canyon above Swan Falls power house, *Maguire & Holmgren 26191* (NY, fide Thompson 2005). Owyhee Co.: 10 mi S of Grand View,

Poison Creek, frequent, sand talus below lake sandstone, 5 Jun 1946, *Maguire & Holmgren 26274* (UC). **Oregon**. Malheur Co.: Brogan, 1910, *Cooper s.n.* (WILLU); hillsides of Cottonwood Creek near the Malheur, 20 Jun 1898, *Cusick 1951* (MO, ND-G fide B. Hellenthal, ORE, UC-2 sheets!); ca 4.5 mi SW of Harper, slope of black volcanic gravel, 4 Jul 1952, *Howell 28640* (CAS, OSC, WILLU); small canyon, the mouth 6 mi NNW of Harper, 4.5 mi airline distance NNW, 3000 ft, common on open diatomaceous slopes surrounded by sagebrush, 5 Jun 1978, *Holmgren 8825* (CAS); SW of Harper, 6 km S of Hwy 20 along Squaw Creek, basalt outcrop with dark heavy soil, ca. 900 m, corollas hot pink with yellow throat, 15 Jun 1984, *Joyal 495* (OSC); ca. 8 km SW of Harper, N of Malheur River on low, rocky hills with numerous welded tuff outcrops, 900-925 m, frequent in black soils, 16 Jun 1984, *Joyal 508* (OSC); "Mathew" [Malheur] Butte, 800 m, sandy soil, 12 May 1896, *Leiberg 2028* (OSC, PH, UC); Brogan, along irrigation ditch, 23 Jun 1910, *Peck 5640* (WILLU); Brogan, along irrigation ditch, 1 Jul 1910, *Peck 5641* (WILLU); 11 mi SE of Vale, dry sandy slope, 19 Jun 1942, *Peck 21283* (WILLU); 5 mi NW of Harper, dry volcanic ash slope, 20 Jun 1942, *Peck 21321* (WILLU); hills 4 mi W of Harper, volcanic sand along gully, 2400 ft, 6 Jun 1944, *Ripley & Barneby 6122* (CAS); 6.6 road mi W of Harper-Westfall turnoff along Hwy 20, then 3.7 mi S of Hwy 20 along Squaw Creek Road, E side of road, on fine black gravels at margins of the bed of a small wash crossing road at this point, 3000 ft, 28 Jul 1988, *Thompson 984* (OSC, UC).

Examples of typical *Diplacus nanus* closely sympatric with typical *D. cusickii*. **Oregon**. Malheur Co.: 11 mi SW of Vale, barren, sandy E slopes in sagebrush country, along road to Harper, ca. 2500 ft, 4 May 1959, *Cronquist 8182* (CAS); hills near Vale, loose warm soil, 8 May 1927, *Henderson 9123* (CAS).

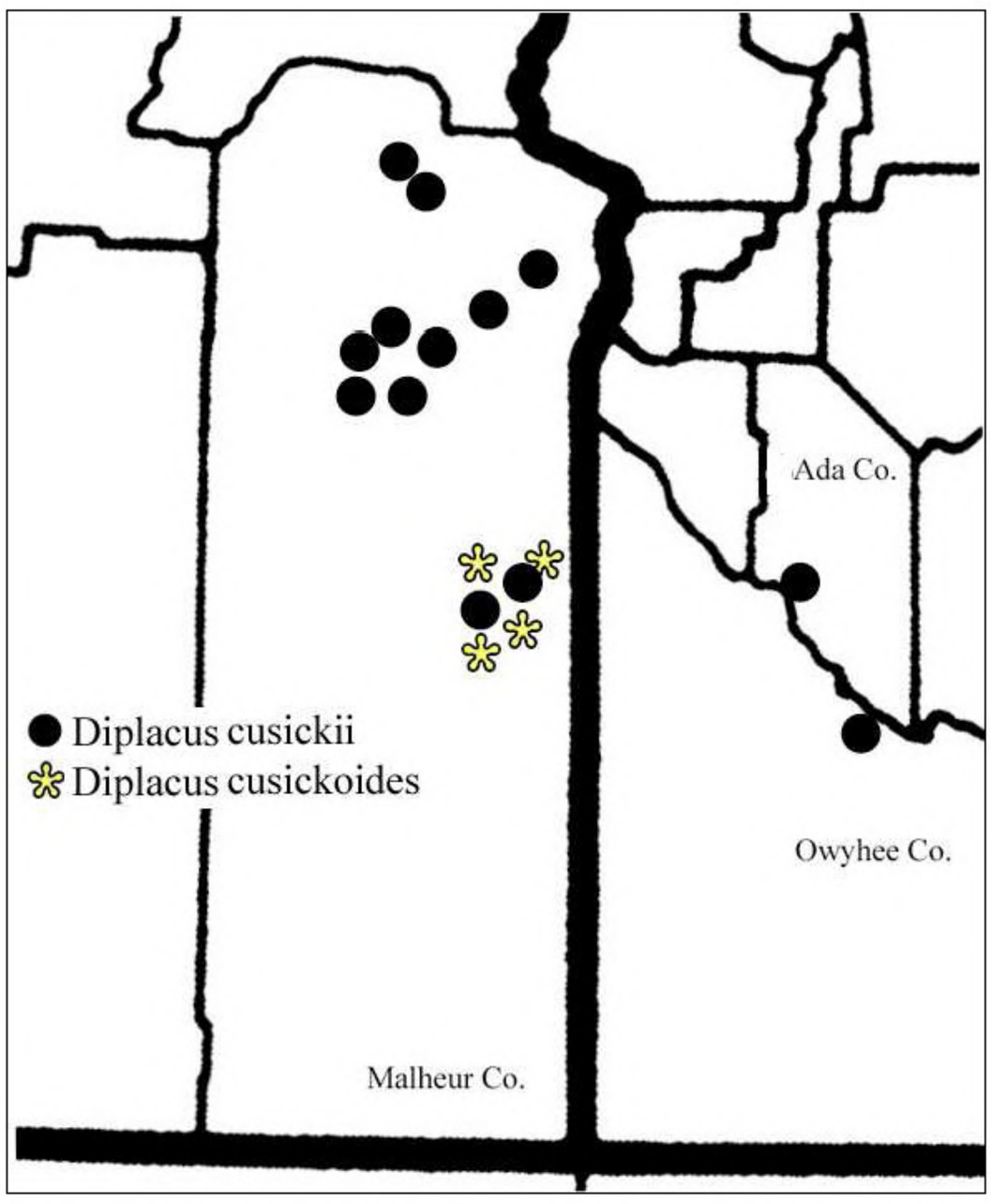

Figure 1. Distribution of *Diplacus cusickii* and *D. cusickioides* in Malheur Co., Oregon, and Ada and Owyhee cos. of adjacent Idaho.

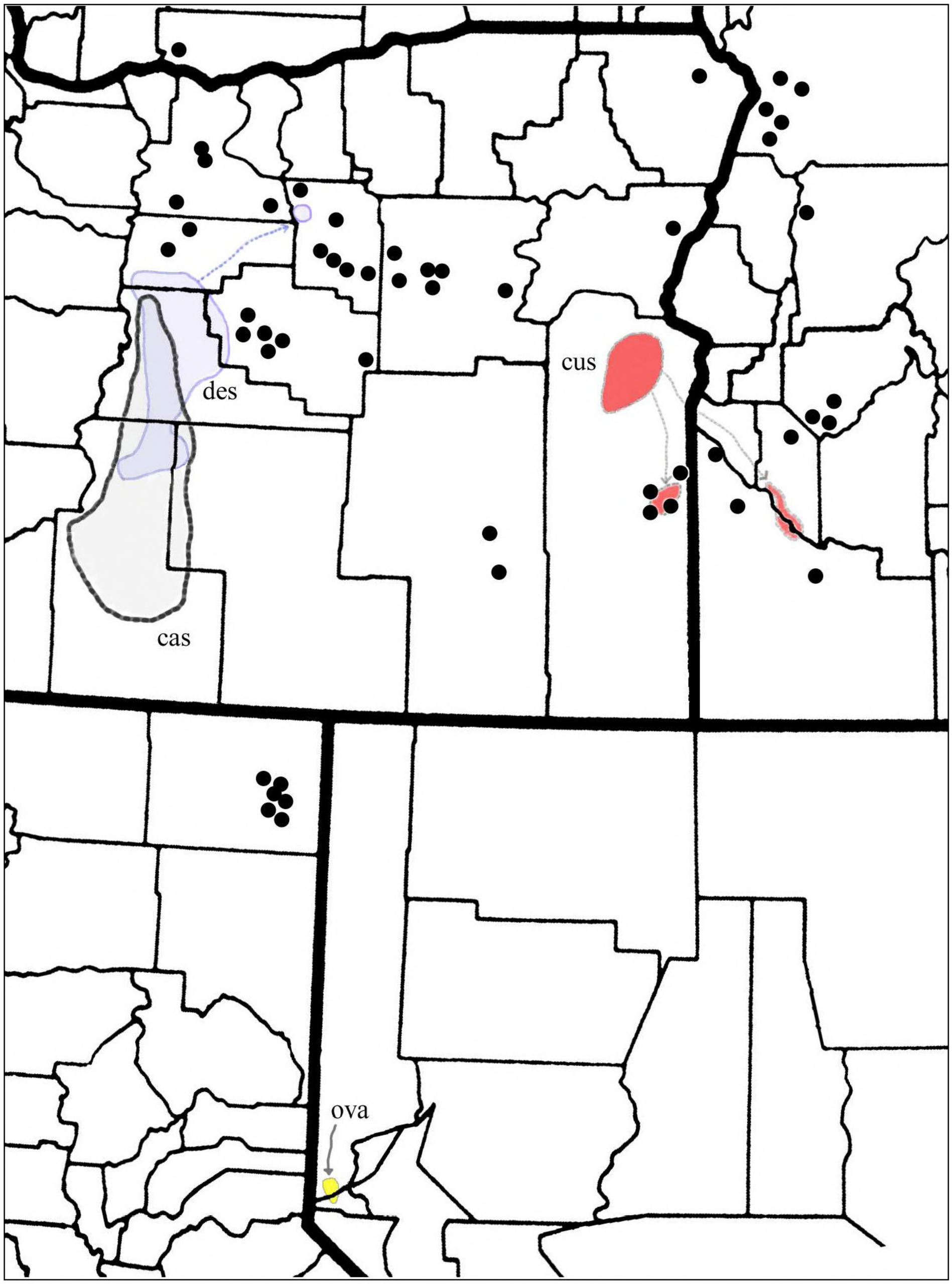

Figure 2. Distribution of *Diplacus cusickioides* (black dots), *D. cusickii* (cus), *D. cascadensis* (cas), *D. deschutesensis* (des), and *D. ovatus* (ova).

Figure 3. *Diplacus cusickioides*. Representative collection, Harney Co., Oregon.

DIPLACUS CUSICKIOIDES Nesom, **sp. nov. TYPE**: **USA**. **Oregon**. Harney Co.: Diamond Craters, N end Steins Mountain, crater rim, lava soil, *Artemisia*, 4500 ft, 12 Aug 1935, *P. Train 107* (holotype: OSC!).

Similar to *Diplacus cusickii* Greene in its mostly ovate to obovate leaves with abruptly and sharply acuminate apices and strongly 2-lipped, magenta corollas; different in its densely villous-glandular stems and leaves.

Annual herbs, taprooted. **Stems** erect to erect-ascending, (1–)3–24(–35) cm, usually simple or few-branched, densely villous-glandular with vitreous, gland-tipped hairs (0.2–)0.4–1.1 mm long. **Leaves** basal and cauline or mostly cauline, (10–)15–25(–35) mm x 4–16 mm, relatively even-sized or gradually larger distally, congested at crowded distal nodes, blades ovate to broadly elliptic-ovate, proximal with a short petiole-like base 1–5 mm, midstem and distal sessile, margins entire, villous-glandular, apex acuminate to a sharp point, both surfaces densely villous-glandular with vitreous, gland-tipped hairs (0.2–)0.4–1.1. mm long. **Flowers** (1–)2 per node, chasmogamous. **Fruiting pedicels** 1–1.5 mm. **Calyces** 7–12 mm, not inflated in fruit, glabrous to minutely (microscopically) stipitate-glandular, lobes triangular-acuminate, unequal, usually falcate-spreading, apices linear-acuminate, sharp-pointed. **Corolla** magenta or rose-purple, tube yellow, throat usually yellow, throat and distal tube red-spotted on floor, palate ridges yellow, densely villous, tube-throat 13–16(–19) mm, floor hairy with fine hairs, limb 14–26 mm wide, distinctly 2-lipped. **Anthers** included, glabrous to sparsely hirsutulous. **Style** pubescent, at least on distal half, stigma slightly exserted, lobes subequal, slightly longer than upper anthers (herkogamous), lobe margins densely short-ciliate. **Capsules** 10–17 mm, usually exceeding calyx.

Flowering May–Aug. Lava formations, steep slopes, roadsides, volcanic gravels, scree, ash; (400–)600–1500(–2000) m; California, Idaho, Washington. See Figure 2 for total distribution.

Figure 4. Probably *Diplacus cusickioides*. From Post-Izee Hwy, east of Prineville, Crook Co., Oregon — area where the range of *D. cusickioides* approaches that of *D. deschutesensis*. Photo by Marvin Kellar, 17 Jul 2007, posted as *Mimulus cusickii* on the Sauntering Oregon website (http://www.saunteringoregon.com/).

Figure 5. *Diplacus deschutesensis*. Isotype, OSC.

DIPLACUS DESCHUTESENSIS Nesom, **sp. nov. TYPE: USA. Oregon**. Crook Co.: sands of the Walker Basin, 1 Sep 1902, *W.C. Cusick 3009* (holotype: MO!; isotypes: DS!, ORE!, UC!).

Similar to *Diplacus cusickii* and *D. cusickioides* in mostly ovate to obovate leaves with abruptly and sharply acuminate apices, magenta corollas with yellow palate ridges, and leaves congested at crowded distal nodes; different from *D. cusickioides* in its smaller leaves with glabrous surfaces and smaller flowers and fruits; different from *D. cusickii* in its smaller leaves, flowers, and fruits.

Annual herbs, taprooted. **Stems** erect to erect-ascending, 4–15 cm, minutely puberulent with gland-tipped hairs. **Leaves** mostly cauline, 10–15(–25) mm x 4–13 mm, relatively even-sized or gradually larger distally, congested at crowded distal nodes, blades broadly ovate or obovate to elliptic-ovate, elliptic-oblanceolate, proximal with a short petiole-like base, becoming sessile distally, sessile, margins entire, with a narrow indurate rim in the distal third, apex at least of distal abruptly and sharply acuminate or cuspidate, surface sometimes purplish abaxially, glabrous to sparsely or very sparsely glandular-puberulent, margins minutely glandular. **Flowers** 2 per node or 1–2 per node on a single plant, often from proximalmost to distal nodes, chasmogamous. **Fruiting pedicels** 1–1.5 mm. **Calyx** 7–8 mm, not inflated in fruit, glandular-puberulent, ribs green distally, intercostal areas whitish, lobes subequal, apices linear-acuminate, erect to slightly spreading. **Corolla** light pink to magenta or rose-purple, often with 5 darker narrow lines extending from the throat onto lobe midveins, palate ridges yellow, densely villous, at least proximal tube yellow, tube-throat 8–12 mm, sparsely glandular-puberulent externally, throat floor and lower lip base densely villous, limb 10–16 mm wide, distinctly 2-lipped. **Anthers** included, glabrous to sparsely hirsutulous. **Style** pubescent, at least on distal half; stigma exserted, lobes subequal or the lower slightly larger, lobe margins densely short-ciliate. **Capsule** 7–9 mm, dehiscent. n = 8 (from *Thompson 977*).

Flowering Jun–Sep. Sandy and ashy soil, pumice sand and gravel, red clay slopes, hillsides, roadsides, bare areas, sagebrush, sagebrush-juniper, juniper, yellow pine and lodgepole pine forests; 700–1500 m; Oreg.

Additional collections examined. **Oregon**. Crook Co.: W side of Millican Road between mile marker12 and 13 on the Millican Plateau, *Juniperus occidentalis*, sagebrush, 1057 m, 17 Jul 2003, *Bhatia et al. ORO50-14* (OSC); sands of the desert near Squaw Creek, 13 Jun 1902, *Cusick 2810* (MO, ORE, PH, UC); Powell Buttes, dry sand under scattered *Juniper*, 30 Jun 1938, *Ireland 1182* (ORE); Powell Butte, sagebrush, sandy hillside, 3250 ft, 30 Jun 1938, *Detling 3148* (ORE); Prineville, dry hillsides, 20 May 1910, *Sweetser s.n.* (ORE). Deschutes Co.: near LaPine, open pine forests, 1 Aug 1922, *Abrams 9647* (DS); Lava Butte, near and S of Bend, easterly cinder slope, common everywhere in surrounding pumice sand, flring from early spring until winter, 29 Sep 1937, *Applegate 11568* (DS, UC); along US Hwy 26, 3.2 mi W of jct with Hwy 20 at Sisters, ponderosa pine-juniper area, 3200 ft, 30 Jun 1961, *Bacigalupi 7923* (JEPS); Lava Butte, 5 Sep 1938, *Beach & Farnham* 74 (OSC); near Sisters, sandy dried soil of yellow pine forest, 3000 ft, 20 Jul 1930, *Benson 2254* (MO); near LaPine, edge of hwy, 24 Jul 1982, *Best s.n.* (CAS); 1.4 mi N of Sisters, on road to Indian Ford development, loose soil in open woods of young ponderosa pine-juniper, 26 Jun 1988, *Chambers 5411* (OSC, UC); ca. 6 mi E of Bend along Hwy 20, 21 Aug 1953, *Clarkson 208* (OSC); 2 mi NE of Lava Butte, pumice soil, common on roadsides and bare areas, 16 Jul 1956, *Costello s.n.* (OSC); LaPine, in volcanic ash, 13 Jul 1925, *Degener 18256* (PH); Hansen's Resort, Sisters, 30 Aug 1928, *Detling s.n.* (ORE); Redmond, sagebrush in sandy soil, 3050 ft, 1 Jul 1928, *Detling 3227* (ORE); 11 mi E of Hwy 20 along Hwy 126, E of Sisters at jct of Buckhorn and Barr roads, sagebrush-juniper, dry sandy soils in open areas, 3000 ft, 28 Jun 1978, *Dwan 1* (OSC); 1 mi W of Sisters, yellow pine forest, 27 Jun 1919, *Ferris & Duthie 560* (DS); ca. 5 mi E of Bend, US Hwy 20, juniper forest, gravel pile, 2 Aug 1955, *Ferris & Lorraine* 13015 (DS, JEPS); between Bend and Sisters, ashy soil, 8 Jul 1928, *Gale 275* (DS, MO); S of Bend, 0.5 mi W of jct of Hwy 97 and Century Drive, edge of lodgepole and ponderosa pine forest, in sand, 4300 ft, *Gentry 2107* (ARIZ, ASU, BRY, CAS, OSC, PH, UC); near Tumalo, sagebrush plains, 8 Jul 1927, *Gilkey s.n.* (OSC); W of Redmond on

Mackenzie hwy, sagebrush prairie, 7 Aug 1927, *Gilkey s.n.* (OSC); near Elk Lake, ash sand at roadside, 28 Jun 1924, *Gilkey s.n.* (OSC); Lava Butte, 8 mi S of Bend, *Gillis 5221* (MIN); 10 mi SE of US Hwy 97 along China Hat Rd (Co. Rd. 18) at jct of road to Skeleton Cave, 1302 m, 26 Aug 1982, *Halse 2558* (OSC); plentiful along US Hwy 97, several mi S of Bend in loose soil derived from pumice, 6 Jul 1940, *Heller 15754* (DS, MO, UC); "Camp Polk," dry pine lands, 5 Aug 1881, *Henderson s.n.* (ORE); 3 mi W of Sisters, undisturbed soil among yellow pines, ca. 3200 ft, 21 Jun 1939, *Hitchcock & Martin 4824* (DS, UC); 1.5 mi N of Sisters, locally common in loose, dry, sandy soil of ponderosa woodland, 3190 ft, 15 Jun 1966, *Holmgren 2711* (UC); road to Tumalo, N of Bend, light volcanic ash, 21 Aug 1938, *Ireland 1292* (ORE); ca. 8 mi S of Bend, 24 Jul 1937, *Jepson 18,468* (JEPS); Black Butte, N of Sisters, dry sandy soil at bottom of butte, 3450 ft, 16 Jun 1960, *Johnson 412* (OSC); 9 mi E of Sisters along Hwy 126 to Redmond, open flat area, juniper-sagebrush, sandy loam, 3000 ft, 30 Jul 1982, *Johnson 570* (OSC); Bend to LaPine, 31 Jul 1931, [with 1 plant of *D. cascadensis*], *Johnston s.n.* (CAS); 8 mi SE of jct Hwys 20 and 28 on Hwy 20, between Tumalo and Sisters, barren flats in juniper-chrysothamnus-purshia-sagebrush association, [mixed collection of *D. deschutesensis* and *D. nanus*], 3 Jul 1950, *Kruckeberg 2061* (UC); 7 mi W of Redmond, 20 Jul 1922, *Lawrence 3404* (OSC); 3 mi N of LaPine, jct of US 97 and Wickiup Reservoir Rd, open lava gravel roadside, 8 Jul 1977, *Lowry 886* (OSC); few mi S of Redmond, road shoulders and adjoining sandy ground, 10 Jul 1938, *McCalla 4911* (DS); 6 mi S of Bend, dry roadside, 17 Aug 1936, *Munz 14437* (CAS-2 sheets, DS, UC); S of Bend along main hwy, 15 Aug 1956, *Parks s.n.* (DS, JEPS, UC); Sisters, 22 Jul 1914, *Peck 5637* (WILLU); 10 mi E of Bend, dry sandy ground, 8 Jul 1937, *Peck 19841* (WILLU); Bend, dry sandy ground, 20 Jul 1927, *Peck 15748* (DS, PH, WILLU); 3-5 mi N of Sisters, gravelly, open pine woods, 3000 ft, 6-8 Jul 1931, *Pennell 15501* (CAS, PH); 10 mi E of Bend on US 20, dry rocky road banks in juniper forest, 3800 ft, 24 Aug 1954, *Porter 6633* (UC); S of Bend, 8 Aug 1935, *Powell s.n.* (SMU, TEX); road to Paulina Lake, Paulina Mts, 0.6 mi E of Dalles-California hwy (US 97), sandy, open flat and scattered *Pinus contorta*, ca. 4200 ft, 2 Aug 1953, *Robbins 3613* (JEPS); 20 mi S of Bend, 26 Jul 1936, *Rose 36685* (CAS); LaPine, 27 Aug 1941, *Rose 41421* (CAS, UC); 6 mi E of Redmond, *Rossbach & Rossbach 533* (DS); S of Bend, roadbed, 17 Jul 1932, *Schreiber 409* (UC); near Bend, 28 Jun 1935, *Sipe s.n.* (ORE); 22 mi S of Bend, sandy roadside, 3 Aug 1949, *Solheim 2635* (DS, PH, TEX); near jct of Hwy 97 with road to Pringle Falls, openings in *Pinus contorta* forest, dry sandy pumice, 4350 ft, 4 Aug 1954, *Steward 6797* (DAV, DS, OSC, PH); between Sisters and Redmond, 23 Aug 1924, *Sweetser s.n.* (ORE); US Hwy 97, at "Y" of Fall River Road, roadside, volcanic sand, 9 Sep 1997, *Sylvester 2508* (BRIT); LaPine Station ca. 1 mi E of Hwy 97 at LaPine, along Burlington Northern RR, open pumice flat bordered by *Pinus contorta-Purshia tridentata*, ca. 4200 ft, 27 Jun 1992, *Taylor 12900* (UC); ca. 4 mi N of LaPine along RR embankment along Hwy 97, yellow pine community, 12 Aug 1966, *Thomas 12373* (DS); Upper Deschutes River, 13 Aug 1925, *J.W. Thompson 335* (DS); 3.3 mi NW of Hwy 126 jct in Sisters along Hwy 20, deep, dusty, ash soil in openings of *Pinus ponderosa* woods, 3250 ft, 27 Jul 1988, *D.W. Thompson 979* (UC); 3.3 mi NW of Hwy 126 jct in Sisters along Hwy 20, deep, dusty, ashy soil in openings of *Pinus ponderosa* woods, 3250 ft, *D.W. Thompson 1020* (UC); between LaPine and Pringle Falls, roadsides, abundant in sandy soil in open places, 4300 ft, 17 Jul 1945, *Weber 2992* (OSC, PH, SMU, UC); Redmond, 25 Aug 1901, *Whited 48* (MO); vicinity of Laidlaw [Tumalo], common on the desert, 6 Jun "1212," *Whited 48* (DS); Laidlaw (Tumalo), dry sagebrush-juniper desert, 8 Jul 1906, *Whited 303*1 (OSC). Jefferson Co.: Metolius River near Camp Sherman, *Dearing 6700* (MACF, SBBG, as cited by Thompson 2005); no specific locality, Jul 1923, *Gale s.n.* (PH); 12 mi SE of Camp Sherman, barren sandy flat in open woods, 8 Jul 1931, *Wherry s.n.* (PH). Klamath Co.: Crescent P.O., sandy roadsides for 2 miles, in places a blanket, 4450 ft, 30 Jul 1959, *Demaree 41410* (SMU); The Timbers, [5 mi SW of LaPine], 39 mi S of Bend, dry pumice sand, for miles along the road, 22 Aug 1950, *Freytag & Van Schaack 3120* (PH); jct of Hwy 58 and Hwy 97, 9-10 mi S of Crescent, thousands of plants growing on cinders along roadsides, 4250 ft, 26 Jul 1988, *Thompson 977*, voucher for chromosome count of $n = 8$ (CHSC, OSC, UC). Lake Co.: Fisher Range, cutover area, Jul 1929, *Ingram 5109* (OSC); near Fort Rock, 8 Jul 1922, *Lawrence s.n.* (OSC). Wheeler Co.:

area, Jul 1929, *Ingram 5109* (OSC); near Fort Rock, 8 Jul 1922, *Lawrence s.n.* (OSC). Wheeler Co.: E slope John Day River valley above Clarno 0.8 mi E of Jct River and Hwy 48, red clay exposed slopes, 30 Jul 1980, *Wagner 4467* (MO). Klamath or Deschutes Co.: Little Deschutes River, 14 Aug 1897, *Coville & Applegate 538* (DS).

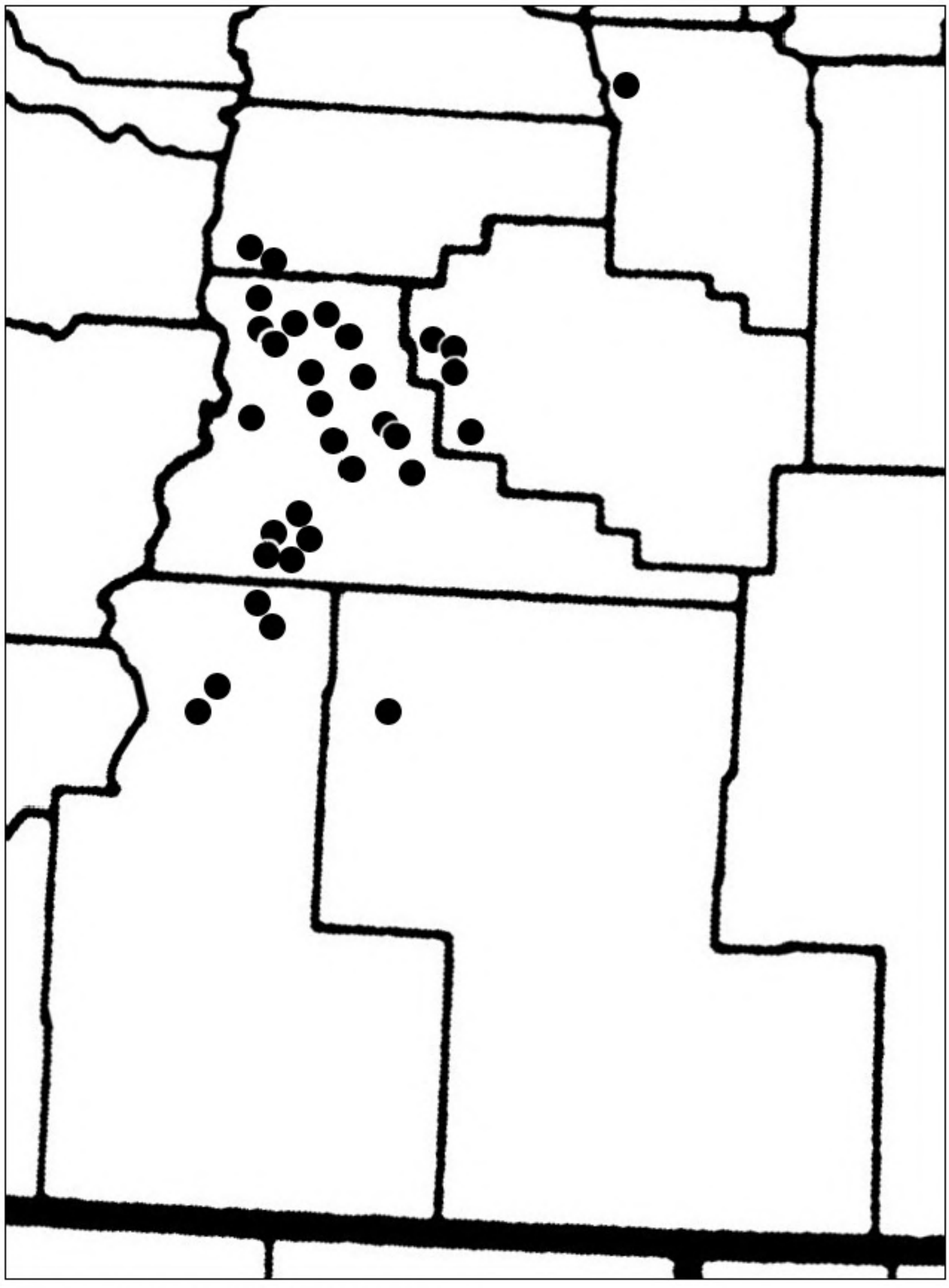

Figure 6. Distribution of *Diplacus deschutesensis*.

Diplacus deschutesensis is known only from Crook, Deschutes, Jefferson, Klamath, Lake, and Wheeler counties of central Oregon. Thompson (2005) regarded these plants as a zone of stabilized hybrids intermediate between *Mimulus cusickii* and typical *M. nanus*. In an earlier study that included both of the latter species, Ezell (1971 and by annotation in 1987) identified the same set of plants simply as *M. cusickii*, not associating them at all with *M. nanus*. Grant (1924, and by annotation of MO collections) identified them variously as either *M. cusickii* or *M. ovatus*. Thompson did not say what features of intermediacy he observed in the "hybrids" but he did note that they produced leaves with acuminate-cuspidate apices and thus would key to *M. cusickii*. The present study finds no unequivocal basis for viewing the evolutionary origin of *D. deschutesensis* as hybrid; presumably Thompson's rationale for this hypothesis alluded to its relatively reduced (more nanus-like) vestiture.

Leaves of *Diplacus deschutesensis* are broad with sharply acuminate apices like those of *D. cusickii* and the corolla coloration also is similar. The flowers (calyx length, corolla tube-throat length, limb width) and capsules of *D. deschutesensis*, however, are considerably smaller and the distal leaves are smaller with glabrous surfaces. Intermediates apparently are few if any.

The *Diplacus deschutesensis* population system lies just outside (west of) the wider range of *D. cusickioides* (Fig. 0). Thompson noted (p. 86) that "the hybrids can occur in vast numbers along roadsides and where [*D.*] *cusickii* [*cusickioides*] is not known to occur. These intermediates may have originally become established by the initial colonization of the area by *M. cusickii* [*D. cusickioides*]. These plants might have been able to flower earlier on the dark (and presumably sun-warmed) volcanic gravels of this region, allowing a greater overlap in flowering periods between the two taxa and resulting in widespread hybridization and stabilization of the resulting hybrid zone."

On the label of *Chambers 5411* (1.4 mi N of Sisters, Deschutes Co.), *Diplacus deschutesensis* was noted to be "Growing intermixed with *M. nanus* (= *D. cascadensis* at this site) but easily identifiable by larger differently lobed corollas and absence of purple spots within the tube. .... Later to begin flowering than *M. nanus*." *Kruckeberg 2061* (between Tumalo and Sisters) is a mixed collection of *D. deschutesensis* and typical *D. nanus*. *Johnston s.n.* (Bend to LaPine, Deschutes Co.) has several plants of *D. deschutesensis* with one of *D. cascadensis*). On the label of *Thompson 978* (Crater Lake, Klamath Co.), a collection of *D. cascadensis*, it was noted that it (as "*D. nanus*") was "intermixed with but far less abundant than [its hybrid with *D. cusickioides* = *D. deschutesensis*] in this area and flowering earlier (with some overlap)."

1. Leaf surfaces glabrous to very sparsely minutely glandular-pubescent, margins minutely glandular; corolla tube-throat 11–15 mm, limb 10–16 mm wide ..... **Diplacus deschutesensis**
1. Leaf surfaces moderately to densely villous-glandular, margins puberulent-glandular to villous-glandular; corolla tube-throat 13–16(–19) mm, limb 14–26 mm wide ..... **Diplacus cusickioides**

Notes on *Diplacus ovatus*

Another entity identified by Thompson (2005) as of hybrid parentage involving *Diplacus cusickioides* occurs in west-central Nevada, though it is far-separated from closest populations of *D. cusickioides* as a putative parent (Fig. 0). Thompson regarded these plants informally as intermediate between *Mimulus cusickii* [*D. cusickioides*] and *M. nanus* var. *mephiticus*, but Nevada biologists have recognized them as a distinct entity and they were formally treated at specific rank as *D. ovatus* (A. Gray) Nesom (Nesom 2012).

Almost all collections of *Diplacus ovatus* have been made near Steamboat Hot Springs south of Reno (Fig. 0). The collection from Big Canyon (*Muñoz 7111*) appears to be slightly south of the

main group of plants; the collection from Carson Hot Springs (*Morefield 5457*) is separated from the main group by about 12–13 miles but is in the same kind of habitat.

Collections examined. **Nevada**. Carson City: Eagle Valley, 0.5 mi S of Carson Hot Springs, 0.5 mi ENE of Lone Mt. summit, NE side of city, open flat granitic alluvial sand, 4690 ft, 12 May 1991, *Morefield 5457* (UC). Washoe Co.: 1 mi W of Reno Hot Springs, gravelly soil, dry desert slopes, 4 Aug 1937, *Archer 5798* (DS, UC); Steamboat Springs, 29 Jul 1907, *Brown s.n.* (CAS); Virginia Range, Geiger Grade (Hwy 17) to Virginia City, loose brownish talus, 5500 ft, 22 Sep 1975, *Crampton 9301* (CAS); Steamboat Springs, dry gravel, 1 Jun 1947, *Delameter s.n.* (DS); Steamboat Springs, 26 Jun 1927, *Eastwood 14855* (CAS); Steamboat Springs, 4700 ft, 15 Sep 1911, *Heller 10361* (CAS, DS, UC); Virginia Range, NV Hwy 17, Geiger Grade, 2.7 mi E of US Hwy 395, 6 mi NW of Virginia City, locally common on pale orange, gravelly slopes with occasional Jeffrey pine, 6200 ft, 18 May 1978, *Holmgren 8705* (CAS); near Steamboat Springs, 5 Aug 1938, *Howell 14250* (CAS); Steamboat Springs, mineralized slopes, 4600 ft, 20 Jun 1962, *Howell 37992* (CAS); Steamboat Springs, mineralized soil, 4600 ft, 28 Jun 1971, *Howell & True 48128* (CAS); Steamboat Springs, 9 Aug 1906, *Kennedy 1487* (CAS, DS); Steamboat Springs, E slope of Carson Range directly E of Mt. Rose, with *Pinus jeffreyi*, 5500 ft, 20 Oct 1982, *Lavin 4353* (CAS); Carson Range, Big Canyon, Washoe Valley, 1707 m, 23 Jun 1967, *Muñoz 7111* (CAS); near Reno, Steamboat Hot Springs, SW of jct of hwys 395 and 27, 27 Jun 1957, *Ornduff 4214* (JEPS); Reno Hot Springs, 1/4 mi S of jct to Virginia City, hydrothermically altered area, sandy soil, joint pine-sagebrush, 5500 ft, 21 Jun 1964, *Pechen 31* (JEPS); Reno Hot Springs, 10 mi S of Reno, intersection of hwys to Mt. Rose and Virginia City, along Hwy 395, hydrothermically altered soil, highly acid, dry and gravelly, 4500 ft, "a few white-flowered," 5 Jul 1965, *Sweeney & Savage 64-11* (JEPS); 2.8-2.9 mi E of Hwy 395 along Geiger Grade road (Hwy 341) to Virginia City, on large travertine slide area on S side of road, common on W end of slide, 5200 ft, 20 Jul 1988, *Thompson 970*, voucher for chromosome count of *n* = 8 (ORE, OSC, US); Steamboat Springs, 6 Jun 1930, *Van Dyke s.n.* (CAS); Geiger Grade, between Steamboat Hot Springs and Virginia City, 5000 ft, 11 Oct 1972, *Williams s.n.* (JEPS); Geiger Grade, abundant on road cuts, 5200 ft, blooms over long period, 23 Aug 1977, *Williams & Tiehm 77-89* (CAS).

Key to the species with leaf apices acuminate to a sharp point

The *Diplacus* species with leaf apices acuminate to a sharp point can be distinguished by the following set of contrasts.

1. Leaf surfaces glandular-villous, margins glandular-puberulent.

2. Stems 2–14 cm, usually highly branched; calyces 7–9(–10) mm; corolla tube-throat 9–11 mm, limb 12–15 mm wide; capsules 6–8 mm, not exceeding the calyx; Carson City and Washoe Co., Nevada ..... **Diplacus ovatus**

2. Stems (1–)3–24(–35) cm, usually simple or few-branched; calyces 7–12 mm; corolla tube-throat 13–16(–19) mm, limb 14–26 mm wide; capsules 10–17 mm, usually exceeding calyx; various counties in Oregon and Modoc Co., California ..... **Diplacus cusickioides**

1. Leaf surfaces glabrous to sparsely glandular-puberulent, margins minutely glandular.

3. Corolla tube-throat 8–12 mm, limb 10–16 mm wide; cauline leaves 10–15(–25) mm; Crook, Deschutes, Jefferson, Klamath, Lake, and Wheeler cos., Oregon ..... **Diplacus deschutesensis**

3. Corolla tube throat 13–16(–19) mm, limb 16–24 mm wide; cauline leaves (10–)15–25(–35) Malheur Co., Oregon, and Ada Co., Idaho ..... **Diplacus cusickii**

A new species segregated from *Diplacus nanus*

Wayland Ezell, in his Ph.D. dissertation (1971), proposed to formally recognize the population system named below as *Diplacus cascadensis* as well as that of *Diplacus jepsonii* as "ecogeographic races" at subspecific rank within *Mimulus nanus*. Ezell, however, never took his study further (apparently not even distributing his vouchers) and his proposal was never otherwise published. He noted (p. 67) that "At the limited zones of contact of typical [*Diplacus nanus*] and [*D. cascadensis*] in central Deschutes County (*Ezell 100, 140*), intergrades, as well as typical parental types of each, occur sympatrically, thus indicating that natural hybridization takes place." He observed good seed set in experimental hybrids between the two entities, supporting his hypothesis of gene flow.

Diplacus nanus and *D. cascadensis* both appear to be entities of consistent morphology and distinct geography. Putative natural hybrids and intergrades between them are few and geographically localized, mainly in northern Deschutes County, where the two are closely sympatric (Fig. 7). The collection cited and mapped as *D. cascadensis* from southeastern Lake County (*Crosby 1856*) is out of range and earlier flowering and may represent an independently derived hybrid between *D. nanus* and *D. cusickioides*.

1. Distal leaves obovate to broadly oblanceolate, mostly 5–8(–12) mm wide; corolla tube-throat 8–10 mm, proximal tube purple, lower lip glabrous; mature capsule 5–8 mm ..... **Diplacus cascadensis**
1. Distal leaves oblanceolate to elliptic-lanceolate, mostly 2–4 mm wide; corolla tube-throat 11–14 mm, proximal tube yellow or purple, lower lip sparsely to densely villous; mature capsule 8–12 mm .. .. **Diplacus nanus**

DIPLACUS CASCADENSIS Nesom, **sp. nov.** **TYPE: USA. Oregon.** Deschutes Co.: very common in loose soil along US Hwy 97 for several miles near LaPine, Transition Life Zone, 6 Jul 1940, *A.A. Heller 15756* (holotype: MO!; isotypes: CAS!, UC!).

Similar to *Diplacus nanus* in its purplish leaves congested on crowded distal nodes, minutely glandular-puberulent vestiture, purplish, strongly 2-lipped corollas; different in its broader distal leaves, shorter calyces, shorter corollas with glabrous throat and magenta tube, and shorter capsules.

Annual herbs. **Stems** erect to ascending-erect, 2–10 cm, short-glandular-villous to glandular-puberulent with gland-tipped hairs. **Leaves** mostly cauline, basal early deciduous, 10–22 mm x 2–10 mm, relatively even-sized, blades elliptic-spatulate proximally, becoming sessile distally, obovate to broadly oblanceolate, distal mostly 5–8(–12) mm wide, congested on crowded distal nodes, margins entire, apex obtuse to rounded-acute, surfaces green or one or both often purplish, minutely glandular-puberulent. **Flowers** 2 per node or 1–2 per node on a single plant, chasmogamous. **Fruiting pedicels** 1–3 mm. **Calyx** (4–)5–7 mm, not inflated in fruit, glandular-puberulent, ribs dark green or reddish, intercostal areas whitish, lobes subequal, apices acute to acuminate. **Corolla** marcescent, magenta to purplish with a dark purple line extending out along the middle of each lobe, palate ridges yellow with red spots, tube dark purple, tube throat 8–10 mm, glabrous externally, throat floor glabrous, limb 7–11 mm wide, distinctly 2-lipped. **Anthers** included, minutely viscid-villosulous. **Style** apparently glabrous; stigma exserted, lobes equal to subequal. **Capsule** 5–8(–9) mm, barely exserted or even with calyx lobe apices, dehiscent. $n = 8$ (from Ezell populations NC-108 and NC-130; Ezell 1971; *Thompson 978*).

Flowering Jun–Aug. Open pumice flats, screes, sandy soil, juniper-sagebrush, juniper, pine-juniper, yellow pine and lodgepole pine forests, roadsides; 1400–2400(–2600) m; Oreg.

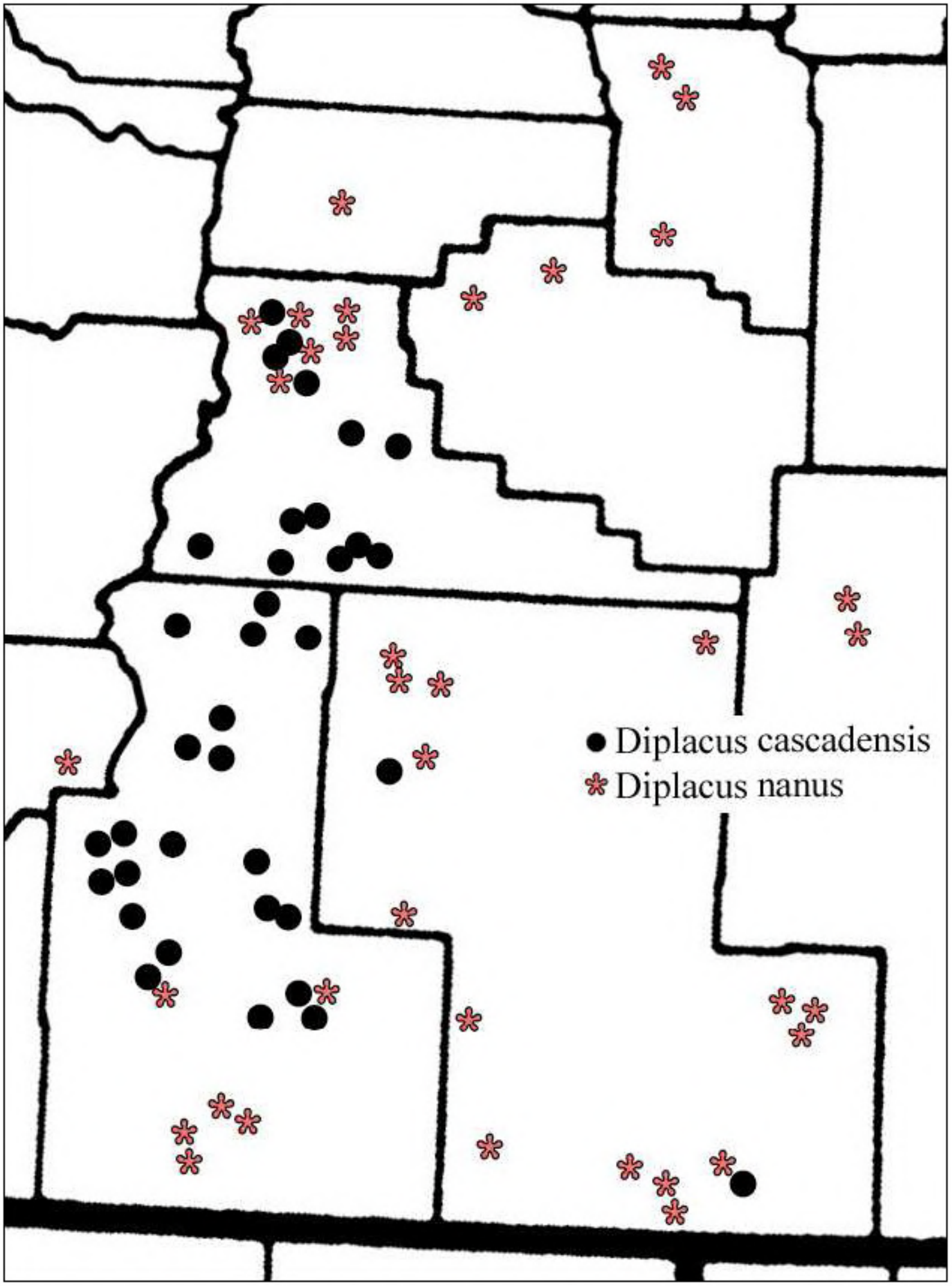

Figure 7. Distribution of *Diplacus cascadensis* and typical *D. nanus* (in the range of *D. cascadensis*). Localities for *D. nanus* all from ORE-OSC-WILLU.

Figure 8. *Diplacus cascadensis*. Representative collection, Klamath Co., Oregon.

Figure 9. *Diplacus cascadensis*. Crater Lake National Park, Oregon, 1 Jul 1956. Photo by Charles Webber©California Academy of Sciences. CalAcademy slide # T 8203, posted on CalPhotos as *Mimulus nanus*.

Additional collections examined. Oregon. Deschutes Co.: Sisters, sagebrush and juniper covered plains, sandy soil, 8 Jun 1930, *Applegate 6168* (DS); between LaPine and Fort Rock, lodgepole pine forest, 29 Jun 1932, *Applegate 7360* (DS); along US Hwy 26, 3.2 mi W of its jct with US Hwy 20 at Sisters, ca. 3200 ft, *Pinus ponderosa-Juniperus* forest, 30 Jun 1961, *Bacigalupi 7919* (JEPS); Juniper Waysides, between Redmond and Sisters, very common in clear spots between sage in juniper-sage zone, sandy loam, 26 May 1956, *Barkley 54* (CAS, OSC, SMU); 2.7 mi S of Sisters on Hwy 20, open woods of *Pinus ponderosa* with *Juniperus occidentalis* and *Purshia*, scattered in bare sandy soil, 14 Jun 1971, *Chambers 3103* (OSC); Paulina Mts, gravelly hillsides, 6900 ft, 20 Jun [flr] and 29 Aug [frt] 1928, *Detling 95* (OSC); East Lake in Deschutes Natl. Forest, dry sand, 28 Aug 1928, *Detling s.n.* (ORE); Sisters, sandy, grassy slopes, 11 Jun 1925, *Gorman s.n.* (ORE); Crater Lake, 7 Aug 1938, *A.L. Grant s.n.* (UC); along Camp Polk road, 0.5 mi N of jct with State Hwy 126, ca. 1.8 air mi W of Cloverdale, with *Pinus*, *Purshia*, *Juniperus*, 942 m, 7 Jun 1989, *Halse 3879* (BRIT, CHSC, OSC); Deschute's bridge, 19 Jun 1885, *Howell s.n.* (OSC); obsidian flow between East and Paulina Lakes, 30 Jun 1931, *Howell 7081* (CAS); ca. 2 mi S of LaPine, 24 Jul 1937, *Jepson 18467* (JEPS); 1/2 mi E of Hwy 20 on Innes Market Road, *Juniperus occidentalis* woodland, deep sandy soil, 18 Jun 1990, *Kaye 1238* (OSC); 38.8 mi from Bend on Fort Rock road, just SW of China Hat, 28 Jul 1919, *Lawrence 2452* (OSC); E of Bend, 1 Jul 1927, *Lawrence 4049* (OSC); 5 mi S of Bend, common in sandy soil in cutover yellow pine woodland, *Purshia* dominant, 19 Jun 1946, *Maguire & Holmgren 26464* (DS); S of Wake Butte, dry pumice sand in frost bowl, ca. 4240 ft, 18 Jul 1991, *Mastrogiuseppe 6215* (OSC); 2 mi S of LaPine, [ca. 4270 ft], 17 Aug 1936, *Munz 14428* (CAS, DS); Sisters, 22 Jul 1914, *Peck 5638* (WILLU); LaPine, dry woods, 23 Jul 1920, *Peck 9628* (WILLU). Klamath Co.: Crater Lake Natl. Park, Cloud Gap, 4-5 Aug 1922, *Abrams 9807* (DS); Wine Glass, N brink of Crater Lake, deep pumice sand, 15 Jul 1924, *Applegate 4108* (CAS, PH);

Sprague River 5 mi above Chiloquin, lodgepole pine woods, 28 Aug 1925, *Applegate 4532* (DS); E rim of Crater Lake, Skell Head, dry pumice, 1 Aug 1934, *Applegate 9171* (DS); Sentinel Point, pumice slopes and about the rim, Crater Lake Natl. Park, 12 Aug 1949, *Baker 6293* (OSC, UC); E side of Crater Lake, Rim Road, Jul 1924, *Baker 668b* (UC); mouth of Crater Lake, 23 Jul 1982, *Best s.n.* (CAS); ca. 16 km S of LaPine, roadside ca. 0.8 km W of Hwy 31, 1291 m, 1 Aug 2003, *Bhatia et al. ORO50-23* (OSC); Hwy 97, 3.7 mi S of jct with Hwy 31 S of LaPine and 1.3 mi S of Deschutes Co. line, *Pinus contorta/Purshia tridentata* community, in soft, moist, ashy soil by a drainage channel along the hwy, open bare area, 3 Aug 1985, *Chambers 5236* (CAS, ORE, OSC); Crater Lake, 1 Aug 1913, *Coombs s.n.* (CAS); Williamson River, dry hillside, 25 Jun 1931, *Evans 320* (PH); 0.5 mi S of entrance to West Davis Lake public campsite, in lodgepole pine forest, 4400 ft, 12 Jul 1968, *Ezell 108* (OSC); Crater Lake Natl. Park, Skells Point, pumice-covered flats, 15 Aug 1941, *Ferris & Lorraine 10637A* (DS); Hwy 31 ca. 8.2 mi SE of jct with Hwy 97, sandy soil, 1335 m, 29 Jun 2010, Halse 7998 (OSC); Hwy 97 at milepost 232, pumice-gravel roadside, 1371 m, 20 Aug 2012, *Halse 8660* (OSC); Winema Natl. Forest, Devil's Garden Geological Area, bare pumice in the explosion crater, 1 Jul 1982, *Heath s.n.* (OSC); Crater Lake Natl. Park, lookout above Skell Head, E side of Lake, pumice area next to parking lot, 7150 ft, 17 Jul 1966, *Holmgren 2899* (UC); Crater Lake NP, Skell Head, sandy volcanic soil, 7140 ft, 12 Oct 1962, *Ireland 3222* (ORE); Crater Lake, 31 Jul 1931, *Johnston s.n.* (CAS); Sand Creek, E of Crater Lake, 31 Jul 1931, *Jones 28830* (CAS, MO, UC); Sun Pass, 25 mi S of Beaver Marsh, volcanic sand surrounded by *Pinus murrayana* woods, 26 Jun 1949, *Keck 6319* (DS); N rim of Crater Lake, pumice and lava flows, 6800-7800 ft, 11-20 Sep 1926, *Kildale 2753a* (DS); N rim of Crater Lake, pumice slope, 15 Jul 1938, *McCalla 4982* (DS); Winema Natl. Forest, 20-22 Jun 1991, *Meinke*—7 collections with locs by township and range (all OSC); 8 mi SE of Odell Lake, 4900 ft, 10 Jun 1941, *Merkle 5* (OSC); near Chiloquin, western yellow pine woods, 4300 ft, 12 Jun 1948, *Merkle 48-13* (OSC); 10 mi S of Crescent, 19 Jul 1920, *Peck 9577* (DS); sandy woods along Klamath Falls-Bend road, 20 mi S of Crescent, 21 Jul 1920, *Peck 9628* [same number as different collection following] (MO); S of Lonroth, gravelly pine flats, 11 Jul 1931, *Pennell 15563* (PH); Crater Lake, pumice sand of NE rim, 7300–7500 ft, 10 Jul 1949, *Pennell 26818* (PH); 6 mi N of Crescent, covering roadside flats, 6 Aug 1955, *Raven 8443* (CAS); Fremont Natl. Forest, Road 3462, ca. 4 mi NE of Spodue Mtn, open area on pumice soil, with *Pinus ponderosa*, *Purshia tridentata*, ca. 5300 ft, 29 Jun 1990, *Rittenhouse 315* (OSC); Crater Lake NP, Cloud Gap, coarse pumice soil, 13 Aug 1951, *Rogers 68* (OSC); Sand Creek, E of Crater Lake, open lodgepole area, 18 Jul 1928, *Sipe s.n.* (DS, MO, OSC); Crater Lake, 14 Aug 1925, *Thompson 137* (DS); alpine pumice slopes of Crater Lake, 7000 ft, 20 Jul 1935, *Thompson 12207* (CAS, MO, UC); Crater Lake Natl. Park, 6.0 mi E of jct with road to Diamond Lake along East Rim Drive, 2.8 road mi NW of Skell Head, hundreds of plants on S end of high bank of bare soft sand above E side of road, 7000 ft, 25 Jul 1988, *Thompson 976* (OSC, UC); jct of Hwy 58 and Hwy 97, 9-10 mi S of Crescent, infrequent on cinders along roadside, 4650 ft, "intermixed with but far less abundant than [its hybrid with *D. cusickioides* = *D. deschutesensis*] in this area and flowering earlier (with some overlap)," 26 Jul 1988, *Thompson 978*, voucher for chromosome count of $n = 8$ (OSC, UC); 2 mi N of Chiloquin turnoff, roadside of Hwy 97, 29 Jun 1977, *Wagner 1369* (ORE, OSC); Crater Lake NP, Cloud Gap, 21 Jul 1928, *Wynd 2286* (ORE); Crater Lake NP, Cloud Gap parking area, near Red Cloud Cliff, Rim Drive, dry steep slope of pumice, 7875 ft, 9Sep 1994, *Zika et al. 12283* (OSC); Crater Lake NP, E side Rim Drive, 0.8 mi W of Wineglass, NW of Roundtop, pumice banks, 6700 ft, 27 Jul 1995, *Zika 12573* (OSC). Lake Co.: 4 mi W of Adel on Hwy 140, 1/3 mi N of hwy, white volcanic soil, 9 May 1978, *Crosby 1856* (OSC); Long Prairie N of Silver Lake, 21 Jun 1919, *Ferris & Duthie 431* (DS).

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